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CONTRIBUTIONS TO THE LIFE HISTORIES OF PLANTS, NO. II.

BY THOMAS MEEHAN.

The leading facts, given in these papers, have been communicated verbally during the year 1888 to the Academy of Natural Sciences of Philadelphia or its Botanical Section. In preparing them for publication, it was believed they might add to the interest of the meeting of the American Association for the Advancement of Science at Cleveland, if read there prior to a full publication here. This statement is necessary to explain the somewhat controversial manner, intended to excite debate, in which the facts are presented. The remarks of those who discussed the papers, are briefly given in the *Botanical Gazette*, for September 1888.

Some new facts in the life History of Yucca.—In the extremely fascinating subject of the relation of insects to flowers no plant possesses a greater interest than the *Yucca*. It is assumed that insects' visits are arranged for cross-fertilization, and this again on the assumption that cross-fertilization must in some way, be a great benefit to the species or to the race. This conclusion is a fair one. Some good has been found from cross-fertilization, and some flowers seem only to produce seed when cross-fertilized,-but in *Yucca* we have the anomaly of a floral structure so arranged that it can scarcely pollinate itself or in any way receive pollen except by artificial aid and yet that arrangement results, in so far as we can see, simply from the use of its own pollen. There is in *Yucca* a more wonderful relation between the insect and the flower fertilized than possibly in any other case. Professor Riley, to whom the great credit of this wonderful discovery is mainly if not wholly due, has well expressed this intimate relation in the insects name *Pronuba yuccasella,* and yet it is evident to those who observe closely the working of this wonderful arrangement, that it has no relation to cross-fertilization, but results in self-fertilization. In most cases, as clearly shown by the observations of Prof. Riley, the pistil receives through the medium of the insect the pollen from its own flower, or at best the pollen from the flowers on the same or adjacent plants; which is equally self-fertilization. Just why this plant should be put to all this trouble to get results through an agent, with no other result than it would obtain if it did the work itself, is surely a problem worthy of any endeavor to solve. Mankind has servants and slaves, and even small insects, drone bees, and other creatures live in indolence by the sweat of other brows. There are many parallels between plants and animals. Is *Yucca* to be a case of absolute servitude on the part of the insect, from sheer indolence on the part of the Yucca to do its own work? It seems to me we shall not be able to draw the veil from this great mystery till we make continuous and careful observations of all the facts in its history, and place them on record for comparison with those which others may make.

Prof. Riley once made the remarkable statement that he had seen the Yucca Moth collect pollen, and thrust it down the tube of the stigma, as if it knew that some such process was necessary to insure fertilization. Dr. Engelmann had found in the Yuccas he examined, that the apex of the pistil was not stigmatic,—the receptive portion was low down in the tube. The two observations, taken together, gave color to the supposed object of the insect. I have shown, (see Proceedings of the Meetings at Cincinnatti, Saratoga and Buffalo,) that pollen applied to the apex in *Y. angustifolia,* and protected by gauze from the insect, resulted in seed just as well as when the work was done by an insect. The tubular character noted by Dr. Engelmann cannot therefore be a constant one; and we shall have to admit that the reasoning of the insect which led it to thrust the pollen down the tube in the other species, leads it to perceive there is no tube in *Y. angustifolia,* and that the application of pollen to the bare apex is sufficient in this species.

Up to this season I had never been able to detect the insect behave in the plants around my house, as Professor Riley saw them behave; but I have always conceded that he is too careful and too close an observer to have been mistaken in such an observation. The record of the act of the insect thrusting its tongue down the stigmatic tube, from so accurate a naturalist, needs no confirmation from any one, however one may be allowed to hold his judgment in suspense as to the object of the insect in such behavior; not then as confirming Prof. Riley, but as part of my observations of this year, I desire to say that I have recently seen an insect at the same task. It worked its proboscis up and down the tube of the pistil, much as a sportsman would load his gun.

I find, in this region *Yucca filamentosa* commenced to bloom this year about the end of June. Some plants will bloom a full week, or occasionally ten days before others, though years ago, all the plants under my notice came from root cuttings of one stock and not from seed. The flowers begin to expand an hour before sun-down, assuming a campanulate form by dark. By sunrise the next morning they are closed, and they remain closed till an hour before sun-set when they again expand, and go through another day as before. But at the third evening's expansion they become almost rotate, closing again the next morning but only to wither and fall away. The flower opens and fades within three days.

During the first week or ten days of the flowering period, an enormous amount of moisture exudes from every part of the flower. It trickles down the outer surface of the perianths, collecting in drops at the apices of the lobes, sometimes almost covering the leaves with spots where the drops have fallen and indicating a somewhat gummy character. The pistil is completely covered with minute bullæ, from which the same kind of liquid exudes. It is not a sweet liquid, indeed differs from pure water only in having a very slight trace of bitterness. The moths become very active just after sunset, traveling up and down rapidly over the moistened stigma, my idea being that they were feeding on the moisture, and that this probability also included the case of the one noted above as thrusting its proboscis down the tube of the stigma. But the insect's motions are so rapid that in the twilight I could not feel absolutely sure of the objects for which they were laboring so hard.[1]

The most interesting part of my observations comes in here. When about half the blossoms on the huge panicle had matured, the production of moisture ceased. On the evening of the eighth of July I could find no trace of an exudation of moisture, nor was there during the whole remainder of the flowering period. Strange to say my friends whose attention was called to this sudden cessation of a watery overflow all suggested, "did you note any peculiar condition of the atmosphere ?" I call attention to this here because it is so common in reasoning on similar phenomena to say the atmosphere was so-and-so *therefore* this or that resulted. It is the bane of exact philosophical deductions that such hasty assumptions are common. We may with more propriety remember that in trees and plants generally a large amount of moisture is stored in the tissue during winter. apparantly ready for the enormous draft on the storage basins which the sudden burst of masses of young foliage must entail in spring. All know how maples and other trees bleed on the slightest wound before the bursting of the leaf,—and how completely destitute of moisture the tissue seems a short time afterwards. All bleeding ceases as the young leaf has fully expanded. Will not the same necessity exist for a provision of moisture for the enormous number of juicy succulent flowers the Yucca has suddenly to produce? May there not be enough and to spare in the earlier period, with none to waste towards the last? These suggestions are all useful as clews to further discoveries. The danger in science is that we rest satisfied with plausibilities, and mistake them for facts.

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[1] This paper was read at the Cleveland meeting of the American Association for the Advancement of Science, where Prof. Riley was present and it is due to this eminent naturalist to say that he insisted on his former view that the sole object of the insect in working down the pistil, was to ensure the fertilization of the flower.

My object is to show that the much discussed *Yucca* is yet a comparatively unexplored field; and that its unknown life-history yet promises to be one of the most interesting subjects the teleologist can possibly give his attention to.

A study of the Hydrangea in relation to cross-fertilization.—That many flowers are arranged for cross-fertilization needs no argument to sustain it, nor is it less certain that some flowers can only be fertilized through the aid of wind or insects. Sprengel, it is well known in the early part of the present century, placed this beyond doubt. The great question is not, do plants generally cross-fertilize, but why do they do it? Mr. Darwin's great work in this connection has been to prove that plants abhor in and in breeding, that the struggle for life is necessarily the chief object of existence, and that cross-fertilization tends to make the race stronger and better fitted to engage in this struggle than close breeding would do. The results of many of Mr. Darwin's experiments sustain his views, as do those of many others; but to my mind just as large a number do not sustain them. Mr. Darwin himself has candidly stated that continuous self-fertilization does not in the least impair the fertility of the race. Mere negative vigor is the leading advantage he finds in crossed plants. (Cross and Self-fertilization, Chap. IX, p. 327.)

It is not my object now to controvert the views of Mr. Darwin, or or of his numerous followers. My view of one object of nature in cross fertilization is to aid in production of variety. I have shown ever since discussion grew warm on these subjects, that variation is essential to the present order of things,—that nature, to be consistent with herself, must provide for variations if for no other purpose than to make variety. I now propose to show by some studies in

Hydrangea, that the variations in the species are of the most contradictory character taken from the stand-point of benefits in the struggle for life; while they are entirely consistent with my view of variation for variety's sake. Our garden Hydrangea from Japan, *Hydrangea hortensis*[1] has the ray florets sterile, or rather it is the lateral florets of the compound cyme, that give the enlarged sepals, and fail to perfect the gynœcium. The terminal florets are fertile. In *H. quercifolia*, all the lateral florets are fertile, and it is only the terminal one that has petaloid sepals and is barren. Will any one assert that these exactly opposite conditions can have any bearing whatever as aids in a struggle for life? Suppose we say that the attractive sepals are given to these species for the purpose of attracting insects, and thus aiding cross-fertilization. With this view we examine the American species *H. arborescens*, and we find barely an attempt to make these enlarged petaloid sepals. There are small ones on a few terminals and this is all. It has made out certainly as well in the great struggle as either of its two brethren. But is it a fact that the showy sepals are given to the plant to attract insects? There is neither pollen nor nectar in the male flowers of *H. hortensis*. They conceal the terminal hermaphrodites, and it is scarcely probable many insects, if any, visit the flowers. In the other two, many insects visit the flowers–so far as my observations go, as many visit the *H. arborescens* without the attractive sepals, as the *H. quercifolia* that makes such a show of them.

Turning to the minute fertile flowers on these two species, we are struck by the immense number of stamens and the enormous number of pollen grains one of these racemose cymes gives us. I estimated the number of stamens on one of *H. quercifolia* at 13,000; shaken over a sheet of dark paper it completely whitens it. It can be carried by the wind everywhere, why should it develop pelatoid sepals to attract insects? Both species have the odor of Hawthorn, but in addition *H. quercifolia* has an enormous yield of nectar, which is apparently not abundant in *H. arborescens*. In spite of all the attractions, the petaloid sepals, the abundance of pollen, the delightful fragrance, the super–abundance of nectar, and the actual visits of numerous insects, the flowers are self-fertilizing. The outer row of five stamens mature pollen simultaneously with the expansion of the petals, which falls at once on the receptive stigmas, some hours after the inner series mature, and ensures that self fertilization which the pollen from the first series may possibly have missed. The only possible aid insects can give is in self-fertilization.

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[1] Franchet and Savatier, insist that Smith's name of *H. hortensis*, has priority over *H. Hortensia*.

It is broadly asserted that we owe to the existence of insects the various forms and colors of flowers with their grateful odors and sweet secretions. Here we have illustrations of the most dissimilar and contradictory variations in a single genus, variations which cover all the leading points called for by the insect–adaptationists, and so far as any argument in common use goes, could have occurred with as much reason if not a single insect ever existed. The facts are absolutely inexplicable on any theory of the survival of the fittest in the struggle for life,—but on my view of the absolute necessity of variation for its own sake, the explanation seems simple enough.

Variation is inseparable from even the closest in–and–in breeding. We are as fully justified in saying that nature abhors a perpetuity of form as that she abhors in-and-in breeding, and we can just as earnestly claim cross-fertilization as an agent in bringing about variation for the sake of variety, as for the reasons usually given, and which we find we cannot apply with consistency in so many cases.

That cross-fertilization aids variation, we may well believe is a sufficient reason for its existence,—without assuming that it has no other office to perform.

On the forms of Lonicera Japonica; with notes on the origin of the forms.—The well-known honeysuckle of our gardens, *Lonicera Japonica* Thunberg, gives three forms of this in general cultivation, supposed to be distinct species. One, known as *L. Halleana*, introduced into America about a quarter of a century ago, I take to be the plant so intended by the author of the original name. It is the plant figured in *Botanical Register*, plate 70. Another is *L. brachybotrya* Asa Gray, a well-known form, preferring to creep and root in the ground, to climbing. The third has been long in cultivation as "Chinese woodbine," a favorite for its rosy, sweet flowers, and is the *L. flexuosa* of Loddiges. All the characters given by the authors of the several names, can be found in different stages and conditions of the same plant. The segments of the corolla in *L. flexuosa* are somewhat narrower than in the other two; and it has a rosy purple tint in the stems, leaves and flowers. The leaves in *L. brachybotrya* are shining, and the hair, being a little shorter, makes the plant seem different. The flowers in all three turn yellow soon after they open.

On account of this change, the plant is known as "Silver and Gold" in Japan.

The flowers open towards evening. At the expansion of the corolla, the stamens and pistil are of equal length. The flower is proterogynous. In the morning the stigmas will adhere, if brought together by their viscid secretions; but the anthers do not disperse pollen till later. The expanded flower remains white or rosy-tinted all the day after opening, and turns yellow the second day, fading the third. The tube of the corolla is about an inch long. On the evening of expansion it contains no honeyed secretion. In the morning the production of nectar is coeval with the bursting of the anther cells, by noon the sweet liquid has risen up the tube for about one-third its length. It continues to flow after the change to yellow; and by evening, the tube is full for half its length, or half an inch. When the flower wholly fades, the sweet secretion, which gives the name of honeysuckle to the family is still there. Amid all these points of uniformity, there are differences in productiveness. The form known as *L. brachybotrya* is abundantly fertile; in occasional instances only do the others bear fruit. This is worth noting. Plants twining on trellises, under exactly the same conditions, vary remarkably in their reproductive powers. Such observations have been made before on other plants, and are the facts regarded as puzzling. Mr. Darwin says:—"They make me believe that some individuals of a species differ from others in their sexual affinities (to use the term employed by Gaertner) like closely allied species of the same genus." (*Cross and Self-fertilization*, Chap. vi, p. 209.)

As the expression "sexual affinity" does not explain anything, and as these three honeysuckles are such very distinct individuals as to have been regarded as distinct species of the same genus, they suggested themselves as offering excellent opportunities for observation as to the influence of anything that could be understood as being in the nature of environment that might account for the origin of their several forms; and especially what part the visits of insects might have had in developing the general form of the whole flower. In the honeysuckle, the tube of the flower attracts prominent attention. The large amount of nectar it contains, gives the name of honeysuckle to the family as already noted, and one cannot help referring to the accepted explanation of the origin of tubular forms. "It may be admitted as almost certain that some structures, such as . . . . a long tubular corolla have been developed in order that certain kinds of insects alone should obtain the nectar." (*Cross-and Self-fertilization, Chap. x, p.* 382.) The honey-bee visits all these forms freely. The honey nearly fills the tube, and bees have no difficulty in collecting freely. It can scarcely be believed that the plant made an effort to exclude short tongued visitors, and that the long tube was the result of that effort, and then secreted so much nectar as to nearly fill the tube by which the short tongued insects could get as much as before the effort was made.

Nor must we lose sight of the supposed objects for which insect visitors are to be encouraged, namely, cross-fertilization.

In order to make no mistake in our conclusions, it is proper to note here, that modern literature has misconceived the whole idea of cross-fertilization. There cannot possibly be any physiological benefit from one flower crossing another on the same plant; but this is about all that is involved in much that is written in connection with the visits of insects. Yet Darwin takes especial pains to explain that this is not cross-fertilization. He says: "cross fertilization always means a cross between distinct plants raised from seeds" (p. 10). Even distinct plants, unless under distinct conditions scarcely constitute crossings in his mind. "The mere act of crossing two distinct plants, which are in some degree inter-related, and which have long been subject to the same conditions does little good" (p. 61). Referring to Compositæ (p. 173) he notes that the florets were "self-fertilized" though with different florets from the same head. On p. 345 he declares "pollen from the same plant is equally injurious or nearly so, as from the same flowers." And, after all, it is difficult to tell what Mr. Darwin really means by "injurious," for the most of his experiments, when in his mind resulting beneficially, referred to vegetative luxuriance, in many little related to those greater vital questions on which the good of the race depends. He distinctly states (p. 327) "there is therefore, no evidence at present, that the fertility of plants goes on diminishing in successive self-fertilized generations, although, there is some rather weak evidence that this does occur with respect to height and growth." Still it is clearly his idea, and evidently the proper one, that the cross-fertilization can only be fairly entertained when the physiological conditions vary in the individuals crossed. Though the honeysuckles referred to are all from cuttings from the one individual in each case introduced, yet being three distinct ones from seed originally, there might be a chance for cross-fertilization when three kinds grew altogether, as in those under my observation.

But I found that the bees, and other short-tongued visiting insects, could not, in any way, aid in fertilizing the flower, when gathering nectar. In these forms, the stamens and pistil are curved upward, so that anthers and stigma are far above the lower lip, on which the insect alights. If any insects aid in cross-fertilization, it must be the pollen-gathering bees, and others; but this will render the speculation in connection with the development of nectar, and the prolongation of the tube in favor of certain classes, of no value, especially in connection with the fact noted, that the short-tongued insects can get the liquid in spite of the prolonged tube.

It is usual, when similar instances in other plants have been noted, to weaken the force of the lessons they teach, by objecting, that many things "may have happened." In this case, it would be urged, that there might be some insects in the native country of these honeysuckles, that we have not here where the plant is introduced; but this would not change the fact, that whatever they may be, they would still be divided into long-tongued and short-tongued classes; and that some bees gather honey only, while others are devoted to collecting pollen; nor would it ignore the fact that the stamens and style are out of the reach of the short-tongued class. It "may be" also urged that after the tube had been lengthened to exclude the short-tongued insect, the plant had subsequently, under excessive excitation from the long-tongued visitors, overdone its work, and supplied more nectar than it had originally given; and then, among the "may be's" often indulged in, is that of a "continuation of effort after the reasons therefor have ceased to exist," and the "progress of development towards a new stage of self-interest."

No one could rationally deny that in the functions of plants, self-interest largely enters. Nor can it be successfully controverted that flower are often wholly dependent on insects for their fertilization. The point I have for some years contended for is, that we need not necessarily be forced to assume that every variation in a plant, or every function in its life-work, is for its special interest. It seems to me absolutely essential to the present order of things, that variety, for mere varieties' sake, should exist quite independently of any other consideration. This may involve the necessity of changing the term "adaptation" to "design" in many cases. At any rate, I am unable to see a reason for the special form and arrangement of parts in the honeysuckle flower, that will accord with prevalent speculations, and am constrained to to believe the plant has been forced to assume them for *variety's sake.*